HORN GROWTH IN MOUNTAIN GOATS (*OREAMNOS AMERICANUS*)

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Horns of bovids are important social organs, their growth is often indicative of population characteristics and habitat quality, but little is known of the factors affecting their growth in individuals. We studied horn growth of 135 (51 males, 84 females) marked mountain goats (*Oreamnos americanus*) in Alberta, Canada, for 9 years. In both sexes, horn growth was quadratic during the first 5 years of life and not significant after 5 years of age. Goats completed 93% of horn growth by 3 years of age. Horns of males grew more than those of females during the first 1.5 years of life. Horns of females grew more than those of males during the third year. Although males maintained longer horns than females because of their longer first increment, adult males had shorter horns than females for a given body size. Males had thicker horns than females at all ages, absolutely or relative to body size. Horn growth early in life was correlated negatively with later growth. Annual growth increments of horns of females aged 4–5 years were affected negatively by lactation. Horn growth was not affected by total rainfall during the vegetation-growing season. Total length and basal circumference of horns were correlated positively with mass, chest girth, and hind-foot length in both males and females. While sexual dimorphism in body mass of mountain goats increases until at least 5 years of age, most dimorphism in horn growth is achieved by 2 years of age. Therefore, body mass of mountain goats may be a more important factor than horn size for male mating success.

Key words: *Oreamnos americanus*, mountain goat, annual growth increment, horn growth, Alberta

Horns of bovids are used by males in intrasexual competition for mates (Alvarez, 1990; Geist, 1966). In most species, females have much smaller horns than males, but the functional significance of female horns is not well understood (Estes, 1991; Packer, 1983). We studied horn growth in marked mountain goats (*Oreamnos americanus*), a species with considerable sexual dimorphism in body mass (Houston et al., 1989), which displays an unusually high level of female-female aggression (Fournier and Festa-Bianchet, 1995) and has pointed and dangerous horns. Horns are used prominently in social interactions by both sexes (Geist, 1967), and a study of their development should provide clues to the role of horns in sexual and social interactions. In particular, if horns are important in sexual selection, one would expect considerable sexual dimorphism and a longer period of horn growth for males than females, as is observed commonly in species where males fight by clashing or wrestling with their horns or antlers (Bubenik and Bubenik, 1990). Mountain goats, however, do not fight through horn contact (Geist, 1964), and the high level of female-female aggression may make horns just as useful for females as for males.

In most Caprinae, horn growth continues throughout life, decreasing with advancing age (Geist, 1971; Koubek and Hrabe, 1983) and stopping during winter in temperate and arctic regions (Bunnell, 1978; Hoefs and Nette, 1982). Horn growth can be affected by numerous intrinsic factors such as earlier horn growth by the same individual (Bayer and Simmons, 1984; Massei et al., 1994; Pérez-Barbería et al., 1996), reproduction (Miura et al., 1987; Festa-Bianchet and Jorgenson, 1994), and genetic variability (Fitzsimmons et al., 1995). Among Rupicaprinae, males generally have been reported to produce longer horns than females, especially during the first few years of life (chamois, *Rupicapra*—Hrabe et al., 1986; Massei et al., 1994; Pérez-Barbería et al., 1996; mountain goat—Cowan and McCrory, 1970; Foster, 1978; Smith, 1988; Japanese serow, *Capricornis crispus*—Miura, 1986), but results for mountain goats have differed among studies and have suffered from erroneous measurements (Foster, 1978) and absence of statistical analyses (Cowan and McCrory, 1970).

Extrinsic factors such as precipitation (Bunnell, 1978; Pérez-Barbería et al., 1996), and geographic area (Cowan and McCrory, 1970; Fandos and Vigal, 1988; Foster, 1978) also may influence horn growth. For example, precipitation was correlated positively with horn growth in several studies of Caprinae, probably because it affected abundance and quality of food (bighorn sheep, *Ovis canadensis*—Picton, 1994; chamois—Pérez-Barbería et al., 1996; Dall sheep, *O. dalli dalli*—Bunnell, 1978; Spanish ibex, *Capra pyrenaica*—Fandos, 1995).

Researchers have reported equations to estimate weight of various ungulates from horn length, because measurements of horns are easier to obtain in the field than measurements of weight and can be collected from carcasses (Gray and Simpson, 1979; Rideout and Worthen, 1975). Bunnell (1980) hypothesised that body weight of mountain goats should be correlated highly with horn length. Although both sexes use their horns to establish dominance relationships, Bunnell (1980) suggested that the correlation between horn size and body weight should be stronger in females than males because females are usually dominant over males outside rut (Chadwick, 1977).

Our objectives were to: 1) document sex- and age-specific patterns of horn growth of mountain goats, 2) examine if early horn growth was correlated positively with early onset of reproduction in females and correlated negatively with subsequent growth (Geist, 1966), and 3) assess the influence of rainfall during the vegetation-growing season and lactation on horn growth of females. We also tested Bunnell's (1980) hypothesis that weight was correlated with horn length, especially in females, and calculated correlation coefficients of length and basal circumference of horns with parameters of body size.

Materials and Methods

Caw Ridge (54°N, 119°W) is one of the front ranges of the Rocky Mountains in west-central Alberta, Canada. It includes alpine grassy slopes, short cliffs, and open subalpine forest at 1,750 to 2,170 m above mean sea level. The population of mountain goats had not been hunted since 1969 and varied from 76 to 114 individuals during our study.

From 1988 to 1997, we marked and measured 135 different goats >1-year-old (51 males, 84 females) during 231 captures. Average capture date was 16 July and ranged from 1 June to 10 October. Goats were captured in remotely-controlled wooden box traps and self-tripping Clover traps (Clover, 1956) that were baited with salt. We drugged adult goats with xylazine hydrochloride, whose effect was reversed by injection of idazoxan (Jorgenson et al., 1990). Côté et al. (in press) provided further details on capture procedures and discussed some of the negative effects of captures on females of reproductive age. Because of those unwanted effects, we reduced the number of captures of adult females after 1993. We determined lactational status of marked females by direct observations of nursing behavior.

Most young were born between 20 May and 10 June. The first distinct annual growth ring was formed at the beginning of the second winter of life, when the goat was ca. 1.5 years old; thereafter, each subsequent ring was formed in early winter (Brandborg, 1955; Smith, 1988).

Age was determined by adding 1 year to the number of distinct rings observed at capture, because trapping started in June and ended before formation of the new annual ring in early winter (Stevens and Houston, 1989). We used a measuring tape to record, to the nearest 1 mm, lengths of total horn and of each annual increment along the outside curve, basal circumference, and circumference of each annulus. For goats >8 years old, we measured only the first 7–8 annuli because other growth rings were indistinct (Brandborg, 1955; Stevens and Houston, 1989). For five goats caught early during the study period, we measured annual growth increments for years before the study started. There was no directional asymmetry in total length (paired *t*-test; $P = 0.5$), or base circumference (paired *t*-test; $P = 0.9$). Therefore, we used the right horn in analyses, unless it was broken (1.7% of horns), in which case we used the left horn.

We weighed goats to the nearest 0.5 kg with a spring scale hung from a tripod and measured chest girth to the closest 0.5 cm directly behind the forelegs using a measuring tape (Rideout and Worthen, 1975). We recorded hind-foot length to the nearest 1 mm along the outside of the leg. Meteorological data were recorded at #8 Mine of Smoky River Coal Limited, ca. 17 km from Caw Ridge at an elevation of 1,525 m.

Statistical analyses.—We assessed effects of age and sex on length and basal circumference of horns with stepwise multiple regression (Sokal and Rohlf, 1981); sex was used as a dummy variable coded as 1 for male and 2 for female. Comparisons between sexes for animals of the same age were conducted with Student's *t*-tests. We used Pearson correlation coefficients (r_p) to measure the correlation of length and basal circumference of horns with weight, chest girth, and hind-foot length. To assess differences among correlation coefficients, we applied the *Z* statistic (Zar, 1984). Because we suspected that rainfall during the vegetation-growing season would increase horn growth (Bunnell, 1978; Pérez-Barbería et al., 1996), we calculated an index of annual horn growth (Bunnell, 1978) and compared it with the total precipitation of each particular year during the vegetation-growing season. The growth index was a measure of the difference between mean annual increment of a specific annulus during a particular year and mean annual increment of the same annulus over all years (Bunnell, 1978). We calculated the growth index for each of the first three horn annuli for all years with data for more than five individuals (1987–1995) (Pérez-Barbería et al., 1996). The first three annuli included most of the inter-individual variance in horn length; an average of 93% of total horn growth of animals ≥6 years old was reached by 3.5 years of age. Because males and females had different horn growth during the first 2.5 years, we did not pool data for both sexes. We used data for females, because we had only 1 year with data for more than five males.

We compared horn growth during the first 3 years of life with age of primiparity (≤4 years or >4 years) using *t*-tests. We also used *t*-tests to compare annual horn increments of 4- and 5-year-old females that were and were not lactating. We restricted our analyses to these two age classes to limit confounding effects of age on horn growth, which were taken into account by subtracting the average horn increment for that age class from each individual (9.7 mm for 4-year-olds and 6.2 mm for 5-year-olds). Because we expected a negative effect of lactation on horn growth (Miura et al. 1987), we used one-tailed *t*-tests for this comparison. To compare horn size between sexes, we used analysis of covariance and *t*-tests of the residuals of linear regression of length and basal circumference of horns on hind-foot length (Sokal and Rohlf, 1981).

RESULTS

The best equations generated by stepwise multiple regressions indicated that age ($P < 0.0001$) and sex ($P < 0.0001$) affected horn length and circumference (Fig. 1). The relationships between age and horn length, and age and horn circumference, were not linear (Fig. 1), and a quadratic age term significantly increased the variance explained by multiple regression ($P < 0.0001$). Horn length in mm was predicted by the equation: $X = 39.93(\text{Age}) - 2.73(\text{Age}^2) - 17.79(\text{Sex}) + 133.54$ ($R^2 = 0.74$, $d.f. = 364$). Basal circumference in mm was predicted by the equation: $X = 13.72(\text{Age}) - 0.92(\text{Age}^2) - 25.63(\text{Sex}) + 115.86$ ($R^2 = 0.77$, $d.f. = 353$). Beyond age 4, however, horn size and age were not related (linear

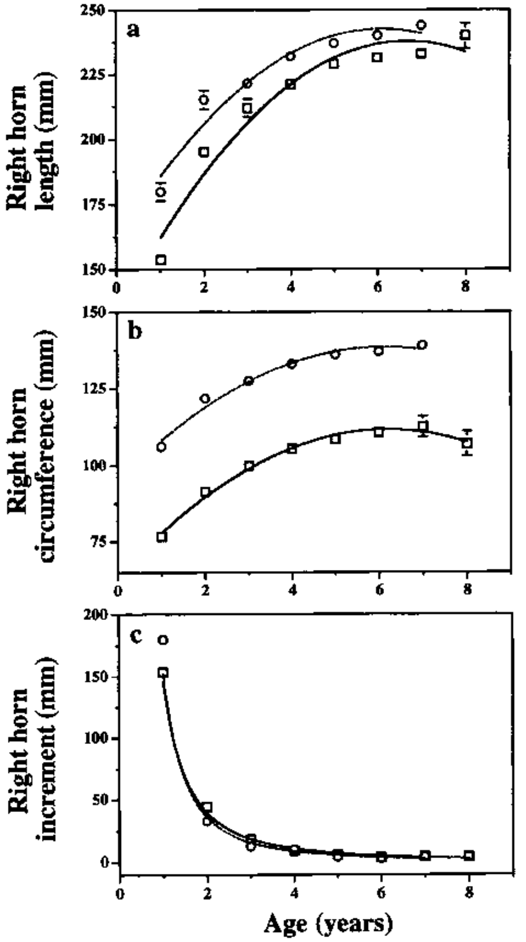

FIG. 1.—a) Average horn length, b) horn circumference, and c) annual horn increment of mountain goats at Caw Ridge, Alberta. Circles and broken lines represent males; squares and continuous lines represent females. *SE* is shown when large enough for the figure's resolution; fitted lines are second-degree polynomial regressions (a and b) and a power function (c) through the averages and are included to visualize differences between males and females.

regression; length–*d.f.* = 124, $P = 0.3$; base–*d.f.* = 121, $P = 0.1$, Fig. 1).

Males had longer first increments than females ($t = 6.4$, *d.f.* = 63, $P < 0.0001$), whereas females grew more horn than males in the following year ($t = 3.5$, *d.f.* = 38, $P = 0.001$, Fig. 1c). Males and females had similar annual horn increments when >3 years old (all $P > 0.1$, n = 26, 24, 19,

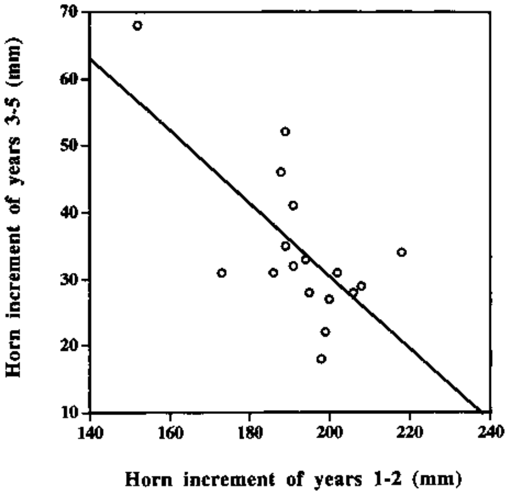

FIG. 2.—Correlation between horn increment during the first 2 years of age and horn increment in the third, fourth, and fifth year of age of female mountain goats at Caw Ridge, Alberta.

13, and 9 for third to seventh annuli, respectively). However, total horn length of males was longer than for females until ≥6 years of age, because males had a longer first increment. Beyond 6 years of age, sex no longer had a significant effect on horn length according to multiple regression (*d.f.* = 88, $P = 0.1$, Fig. 1a). Males had larger horn circumference than females at all ages ($P < 0.0001$, Fig. 1b).

In females, horn growth of the first 2 years was correlated negatively with cumulative growth in the third, fourth, and fifth years ($r_p = -0.67$, $P = 0.003$, Fig. 2). Horn growth of males in the first year was related negatively to growth in the second year ($r_p = -0.62$, $n = 11$, $P = 0.04$) but not to growth in the second, third, and fourth year, although the coefficient was negative ($r_p = -0.66$, $n = 5$, $P = 0.2$). Horn-tip wear appeared to be limited because nine of 17 goats for which we measured length of the first increment at >6 years of age were greater than the average length of the first increment for the population.

Females that produced their first offspring at 3 or 4 years of age did not grow

TABLE 1.—*Correlations* (P < *0.001) of length and basal circumference of horns of mountain goats from Caw Ridge, Alberta, with body-size parameters, 1988–1996.*

Comparisons	Sex	n	r_p	Equations[a]
Horn length versus weight	Males	69	0.801	W = 0.34 HL − 9.19
	Females	123	0.857	W = 0.30 HL − 1.68
Horn length versus chest girth	Males	67	0.850	CG = 0.24 HL + 48.01
	Females	128	0.859	CG = 0.21 HL + 55.52
Horn length versus hind foot length	Males	69	0.886	HF = 0.59 HL + 225.76
	Females	124	0.791	HF = 0.40 HL + 253.48
Horn base circumference versus weight	Males	69	0.793	W = 0.85 HB − 45.40
	Females	124	0.877	W = 1.13 HB − 58.99
Horn base circumference versus chest girth	Males	67	0.760	CG = 0.57 HB + 26.17
	Females	129	0.840	CG = 0.75 HB + 19.56
Horn base circumference versus hind foot length	Males	69	0.867	HF = 1.47 HB + 165.04
	Females	125	0.832	HF = 1.54 HB + 173.76

[a] HL = horn length (mm), HB = horn base (mm), W = weight (kg), CG = chest girth (cm), HF = hind foot length (mm).

longer horns up to 3 years of age ($\bar{X} = 217$ mm ± 16.2 *SD*, $n = 6$) than females that did not produce any offspring until they were >4 years of age (207 mm ± 12.1, $n = 4$, $t = 1.03$, $P = 0.3$). Lactation at 4 or 5 years of age, however, was correlated with smaller horn growth in females (lactating—4.2 mm ± 2.4, $n = 10$; not lactating—11.1 mm ± 7.4, $n = 7$), which represented a significant difference even after accounting for effect of age on horn growth (one-tailed $t = 2.18$, *d.f.* = 15, $P = 0.02$).

The growth index of the first ($r_p = 0.03$, $n = 10$, $P = 0.9$), second ($r_p = 0.17$, $n = 9$, $P = 0.7$), and third ($r_p = 0.20$, $n = 7$, $P = 0.7$) increments was not related to rainfall during the vegetation-growing season. Total length and basal circumference of horns were correlated positively with weight, chest girth, and hind-foot length in both males and females (Table 1, Fig. 3). Second-degree polynomial regressions did not improve significantly any correlation coefficients for males and females ($Z < 1.81$, $P > 0.05$). All correlations were similar for males and females ($Z < 1.85$, $P > 0.05$), apart from the relation between horn length and hind-foot length, where r_p was higher for males than for females ($Z = 2.15$, $P < 0.05$, Fig. 3c).

Analyses of covariance for comparisons in Fig. 3 revealed no effect of sex on horn length with either chest girth or body weight as covariables ($P > 0.5$). Horn length was greater for females than males with hind-foot length as a covariate ($F = 11.38$, *d.f.* = 1,190, $P = 0.001$). A comparison of residuals of linear regression of horn length on hind-foot length showed that, for a given foot length, male horns were ca. 14 mm shorter than female horns. Sex, however, had a significant effect on all analyses of covariance, after accounting for effects of chest girth, body weight, or hind-foot length ($P < 0.001$). Males had thicker horns than females; for a given hind-foot length, horns of males were ca. 11 mm greater in circumference than horns of females.

DISCUSSION

When we considered age and sex together in multiple regression models, we found that length and basal circumference of horns increased with age and were generally greater for males than females. As in chamois (Koubek and Hrabe, 1983, 1984), we found that horn growth of mountain goats was reduced and similar each year at ≥5 years in both sexes. Furthermore, >95% of total horn growth was achieved by age 4. Males had longer horns than females until at least 6 years of age because of their larger size, but when foot length (a skeletal

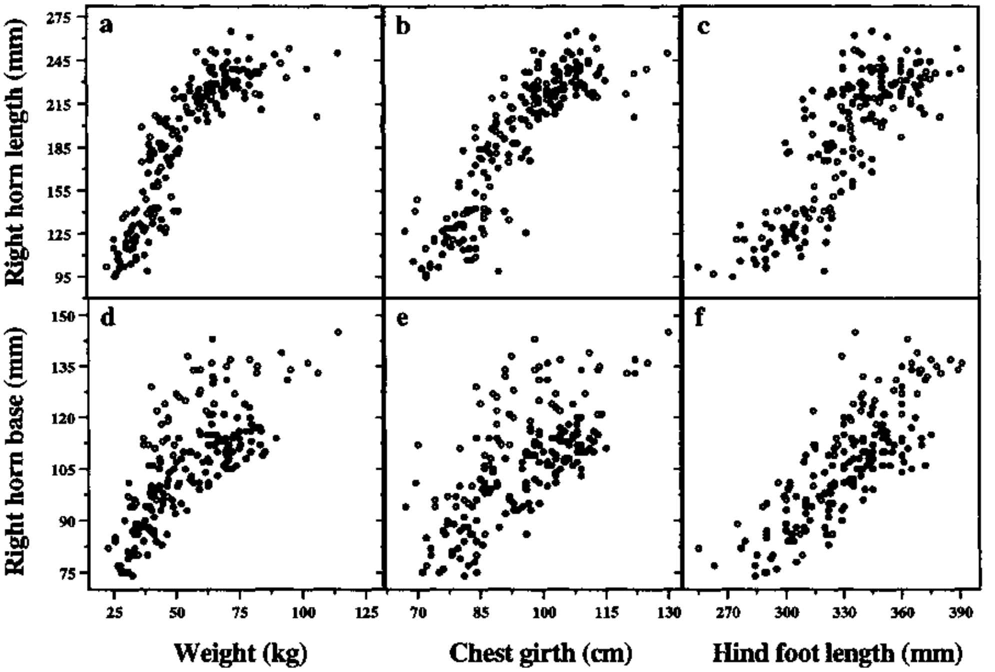

FIG. 3.—Correlations of length (a–c) and basal circumference (d–f) of horns with body measurements of mountain goats at Caw Ridge, Alberta (open circles represent males and filled circles represent females).

measurement indicative of body size) was taken into account, sexual dimorphism was reversed—at a given body size, females had slightly longer horns than males. As Smith (1988) reported for mountain goats in Montana, we found sexual dimorphism in horn circumference at all ages; males produced thicker horns than females (Fig. 1b), even after accounting for body size or mass.

We found that male mountain goats grew longer horns than females until the completion of the first increment, but females grew longer horns than males the following year. The same pattern has been observed in chamois (Hrabe et al., 1986; Koubek and Hrabe, 1984). Cowan and McCrory (1970) also reported a similar trend for two different populations of mountain goats, but they did not present statistical analyses and had small samples. Foster (1978) obtained identical results for goats in British Columbia but expressed doubt about the validity of the measurements that he used. Males and females seemed to adopt a different strategy of horn growth. Females at Caw Ridge did not reproduce until 3–6 years; thus, their lower horn growth during the first 1.5 years probably was not a trade-off with reproduction (Festa-Bianchet et al., 1994). However, it is unclear why male goats, as chamois, had a high horn-growth rate during their first 1.5 years of life, even though they probably do not participate in reproduction until >6 years of age (Koubek and Hrabe, 1984; Lovari and Cosentino, 1986). A possible explanation is that a dominance hierarchy among male mountain goats might be established early in life, and horn size of competing young males may be used to achieve high dominance status that could eventually affect reproductive success (Fournier and Festa-Bianchet, 1995; Thouless and Guinness, 1986).

The greater first increment of horn growth of males compared with females and the opposite for the second increment are consistent with the observation that increased horn growth in the first few years of life is associated with decreased growth during the following years (Bunnell, 1978; Massei et al., 1994; Pérez-Barbería et al., 1996). Our data suggest that there may be an optimal horn size in mountain goats; after that size is attained, there is little or no selective advantage for continued horn growth. The anti-parallel fighting style of mountain goats leads to very rare horn-to-horn contacts (Geist, 1964, 1967), and long horns may not be useful. Also, long horns are possibly weaker and thus easier to break and incur higher thermoregulatory costs (Picard et al., 1994). The thicker, but not longer, horns of mature male mountain goats compared with mature females suggest that stronger horns, resistant to breakage when used to stab the opponent, may be the most useful kind of weapon given the species' fighting style.

We tested the hypothesis that precipitation during the vegetation-growing season, through its effect on plant productivity and quality, positively influences horn growth (Bunnell, 1978; Pérez-Barbería et al., 1996). We did not find such a relationship, but our sample was small. Effect of rainfall and other weather variables, including winter severity, on productivity and quality of vegetation should be monitored in further investigations of horn growth.

Length and basal circumference of horns were correlated with weight, chest girth, and hind-foot length in both sexes. Thus, our horn-growth equations may be used to estimate weight and body-growth patterns from horn measurements (Bunnell, 1980; Pérez-Barbería et al., 1996; Seip and Bunnell, 1984). Estimates would be more reliable for young animals (<4–5 years), because variability of correlations between horn size and body-size parameters appeared to increase with age (Fig. 3). Also, long-term variations in average age-specific length and basal circumference of horns could be used to follow population quality because horn growth usually is related to characteristics of the individual associated with productivity (e.g., weight—Bunnell, 1978; Geist, 1971). We did not find higher correlations between weight and horn length in females than in males, as predicted by Bunnell (1980). Bunnell's suggestion was based on very small samples, and it is unclear if horn length or weight is the best predictor of dominance in female mountain goats (Fournier and Festa-Bianchet, 1995). In males, however, we suggest that body mass may be more important than horn size in determining social rank and reproductive success. Although our study demonstrated that horns of male mountain goats nearly reached an asymptote by 3–4 years of age, body mass continues to increase until ≥6 years of age (Houston et al., 1989).

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